



Research Article

Ecosystem services mapping for municipal policy: ESTIMAP and zoning for urban beekeeping

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Abstract

Pollinating insects are an integral part of cities' natural capital and perform an important ecosystem function with a high degree of relevance to many cultural ecosystem services. Consequently, pollinators serve as a useful proxy for assessing urban biodiversity. Beekeeping has recently emerged as a popular activity in many urban areas and a good deal of the motivation for urban beekeeping for many stems from the *cultural* and *non-consumptive* aspects of beekeeping. Yet the recent increases in domestic honeybee densities in urban landscapes has raised concern regarding the potential threat that honeybees might pose to local populations of threatened bumblebee and solitary bee species. This issue constitutes a trade-off between the *cultural* ecosystem services associated with urban beekeeping and the *regulation and maintenance* ecosystem services of maintaining nursery populations of rare and threatened species. Municipal authorities in Oslo, Norway have proposed establishing eight "precautionary zones", within which placement of honeybee hives could be more strictly regulated. We propose a mapping and assessment approach for informing zoning decisions regarding urban honeybees, utilising a model of an urban landscape's biophysical capacity to support pollinating insects (ESTIMAP). Together with an additional model describing the approximate distribution of

honeybees in Oslo, we identify areas in the city where domestic honeybees may be more likely to exhaust floral resources. This case also tests the policy relevance of ecosystem service mapping tools beyond awareness raising, with broader general lessons for ecosystem mapping and assessment.

Keywords

Ecosystem services, Pollination, Honeybees, Wild bees, Urban, Mapping, Trade-offs

Introduction

Animal-mediated pollination is both an integral ecosystem process and a key ecosystem service (ES). With an estimated 87% of all flowering plant species dependent on insect pollinators for sexual reproduction (Ollerton et al. 2011, Abrol 2012), pollinator-plant relationships may be one of the most ecologically important animal-plant interactions (Kearns and Inouye 1993). The benefits humans derive from pollinators are considerable. Three-quarters of the world's main food crops and over a third of the global food production benefit from animal pollination, with both wild and domestic bees comprising the most important species groups (Klein et al. 2007, Roulston and Goodell 2011). Reports documenting global declines among all key insect pollinator groups—including honeybees, bumblebees and solitary bees—are therefore a source of great concern (Goulson et al. 2008, Potts et al. 2010, Bartomeus et al. 2013). Recent assessments concluded that as many as ten per cent of European wild bee populations are in danger of extinction (Nieto et al. 2014).

The benefits humans derive from insect pollinators extend well beyond food production. Due to the ubiquitous role of insect pollination in sustaining wild plant populations, pollinators are also integral elements in many regulating and cultural ecosystem services. Either directly or indirectly, pollinators contribute to an improved quality of life for many people either through heritage, aesthetics or identity (IPBES 2016). Pollinators and their products are sources of inspiration for art, music, literature, religion, traditions, technology and education (Potts et al. 2016). International agreements for safeguarding cultural heritage explicitly include several of the tangible and intangible heritage values that depend on peoples' interactions with pollinators and pollination webs (UNESCO 2016). The showy flowers that plants produce to attract pollinators are often essential elements in the aesthetics of landscapes, vistas, gardens and parks that contribute to peoples' sense of place (Wratten et al. 2012, Junge et al. 2015).

Few human activities integrate the elements of *provisioning*, *regulating/maintenance* and *cultural* ecosystem services as closely as beekeeping (or apiculture). As a primordial human domestication of nature (Dams and Dams 1977, Roffet-Salque et al. 2016), beekeeping has long been a part of our collective cultural heritage. Recent years have brought a surge in the popularity of smaller-scale urban beekeeping in many European and North American cities. For many, much of the motivation for urban beekeeping stems from the *cultural* and *non-consumptive* aspects of beekeeping (Moore and Kosut 2013).

Over half of world's population and nearly three-quarters of Europe's population lives in cities (United Nations, 2015). The highly modified character of urban areas often limits residents' contact and familiarity with the natural components of ecosystems and the ecological processes that support human societies. Urban apiculture, like urban agriculture, helps re-establish connections between city residents and their natural environment by giving residents an opportunity to actively interact with the ecological processes that produce their food. In many cases, urban beekeeping also provides an opportunity for its practitioners to share their experiences with others and to promote broader support and participation in the stewardship necessary to maintain important ecological functions. This can strengthen local "cultures of nature" (Light 2006) and exemplifies the *relational* values that pertain to how humans can interact collectively with urban ecosystems (Chan et al. 2016).

Public anxiety over the global status of bee populations is another motivating factor driving the recent increase in urban beekeeping's popularity (Alton and Ratnieks 2013, Moore and Kosut 2013). Declining trends in bee abundance is usually attributed to multiple interacting causes, which may vary between wild and managed bee populations (González-Varo et al. 2013, Vanbergen and The Insect Pollinators Initiative 2013). However, there is an emerging consensus that the greatest drivers of pollinator declines are landscape change and agricultural intensification (Carvalho et al. 2013, Carvell et al. 2006, Goulson et al. 2005, Goulson et al. 2010). There is also indication that pollinator species richness generally decreases with increased urbanisation (Ahrné et al. 2009, Bates et al. 2011, Hernandez et al. 2009). Urban environments can in fact sustain diverse assemblages of wild bee species, and species diversity in urban environments is often higher than in the nearby agricultural landscapes (Frankie et al. 2005, Saure 1996, Tommasi et al. 2004, Cane et al. 2006, Matteson and Langellotto 2009). Nonetheless, there is concern that inadequate pollinator abundance may limit reproduction of ornamental, edible, aesthetically desirable or otherwise important plant species in urban areas—often referred to as a *pollinator deficit* (Birkin and Goulson 2015). Many urban beekeepers view their activities as contributions to help ameliorate the potential deficits of local pollinators (Alton and Ratnieks 2013).

Wild bees are often more abundant than honeybees in urban areas (Leong et al. 2014). However, if floral resource availability is the factor which limits urban bee abundance, increasing the number of honeybees in urban areas could have negative effects on cities' wild bee populations. Honeybees have an extremely wide range of flowering plants from which they forage for pollen and nectar (Crane 1990). Honeybees commonly visit a hundred or more different plant species within a single geographic region (Butz Huryn 1997, Coffey and Breen 1997), suggesting a potential for competition with other flower visiting insects. Honeybees can displace foraging bumblebees (Walther-Hellwig et al. 2006), solitary bees (Hudewenz and Klein 2013) and a wide range of flower visiting insects (Lindström et al. 2016, Torné-Noguera et al. 2016). Honeybees' influences on other insects' foraging behaviour can negatively affect wild bee populations, as evidenced by smaller body size (Goulson and Sparrow 2009), and lower reproductive success (Thomson 2004) among bumblebees with nests located near apiaries. Honeybees generally avoid flowering plants with the long corolla tubes that are important resources for many long-tongued

species of bees. However, high bee densities can prompt honeybees to forage among the more marginal resources—thus reducing the nectar and pollen available to the wild bee species which are dependent on such flowers (Ødegaard et al. 2013).

Oslo municipality is home to Norway's capital city. It is also the municipality with the country's highest biodiversity, with the largest number of recorded observations of the country's rare and red-listed species (Henriksen and Hilmo 2015) and numerous habitat types with high levels of local biodiversity. Oslo also features a growing community of urban beekeepers—experiencing a rapid rise in the number of beehive locations since 2012, following the founding of a local chapter of the Norwegian beekeepers association. Norwegian legislation (Klima- og Miljødepartementet 2009) stipulates that government bodies such as the Oslo municipality must act to safeguard against loss of both species and habitat types, with particular emphasis on rare and threatened species. As a precautionary measure to guard against negative effects that high honeybee densities could have on nationally and internationally important biodiversity, Oslo Urban Environmental Agency has proposed establishing eight “precautionary zones” within the municipality, within which placement of honeybee hives could be more strictly regulated. The proposal designates buffers around known locations of rare bee and butterfly species (from recorded observations), as well as sites containing biologically important flowering meadows. The proposed size of these buffers is 1 km: a distance the Urban Environmental Agency selected based on a literature review of honeybee foraging ranges.

Seven of the proposed precautionary zones fall entirely within terrestrial portions of the Oslo municipality, with sizes ranging from 4 to 12 km². The largest of the eight precautionary zones extends over nearly 60 km², covering both the municipality's entire coastline along the Oslo fjord and the many islands located within the municipality's borders. Of the registered beehives located in Oslo in 2016, nearly half fell within these proposed zones. Oslo's Urban Environmental Agency has presented these precautionary zones primarily as a tool for evaluating future applications for beehive permits and has not expressed the intention of demanding the removal of hives that presently fall within precautionary zones. Yet the overlap between the zones and the present location of so many beehives presents a potential for conflict, and both the agency and Oslo's beekeeping community are interested in finding ways to objectively evaluate the appropriateness and necessity of this proposed zoning policy.

The situation in Oslo represents an interesting and illustrative example of a trade-off between biodiversity protection and a cultural ecosystem service. In this paper, we propose a mapping and assessment approach that can help inform zoning decisions regarding urban honeybees, utilising a model of an urban landscape's biophysical capacity to support pollinating insects. As this model describes the spatial distribution of an important indicator of the broader urban biodiversity, the model also constitutes a non-monetary valuation approach (Barton and Harrison 2017), that could be expanded or adapted to apply to either different species groups or different urban planning contexts. Our application of ESTIMAP also tests the degree to which a model originally designed to map and assess ecosystem services at a continental scale may be suitable for modelling pollinators at a local scale, in an urban setting and as a decision-support tool for municipal land use zoning. The paper

demonstrates testing the policy relevance of ecosystem mapping tools beyond the general purpose of awareness raising (Barton et al. in press), by providing some broader general lessons for ecosystem mapping and assessment.

Material and methods

2.1 Study area

Oslo is located in the northern innermost portion of the Oslo Fjord in Eastern Norway (59° 55'N, 10° 45'E). The city itself lies in a south-facing valley, with a local climate characterised by mild winters (average January temperature = -3°C), warm summers (average July temperature = 18°C) and a short but intense growing season (177 frost-free days · yr⁻¹). The terrain slopes gently upwards from sea to the forested hills around the city (300 - 700 m a.s.l.). The Oslo municipality's total area (454 km²) is home to 670 000 residents, which is a 20% increase since 2007 (Oslo kommune 2017). Virtually all of Oslo's inhabitants live within a 147 km² built zone that includes residential, commercial and industrial areas (Oslo kommune 2017). The remaining area (>300 km²) consists of a near continuous forested area extending into neighbouring municipalities to the west, north and east. Mixed boreal forest and deciduous trees cover approximately one-fifth of Oslo's built zone (Oslo kommune 2017) and just over half of the built zone is covered by impermeable surfaces.

2.2 Modelling pollinator habitat suitability

We used a modified version of the ESTIMAP pollination model (Zulian et al. 2013). The original ESTIMAP pollination model was developed for assessment of potential pollinator contributions to agricultural production at the continental scale and follows a similar approach as the InVEST pollination model (Lonsdorf et al. 2009). The continental-scale ESTIMAP pollination model consists of 'Advanced' Multiple-Layer Look Up Tables (Advanced LUT). An Advanced LUT uses a Look Up Table approach to assign values reflecting ES attributes to specific land units, but increases the model complexity through cross tabulation and spatial compositions generated from the overlay of different thematic maps (Schröter et al. 2015). Using both the literature and consultations with experts, model developers generate ES scores to express the relative suitability of land units for pollinating insects in terms of availability of both floral resources and nesting sites. Model inputs also included foraging range and an activity index that represented the effects of local climatic conditions on insect pollinator flight. The initial application of ESTIMAP used CORINE land cover data (CLC2000 in 100 m rasters; EEA 2010), as well as numerous sources of ancillary data (e.g. CAPRI agricultural crops, semi-natural vegetation, low resolution forest maps, gravel roads in agricultural areas), and generated a map of the pollinator potential for the European continent (Zulian et al. 2013).

To model pollinator habitat suitability for a single urban setting, we used spatial data provided by Oslo municipality that defined polygons according to 33 land cover categories—including 14 different forest types (Table 1). We grouped the municipal classifications of

forest types into six broader categories according to expert assessments of the forest attributes that pertain to the life histories of pollinating insects. We then differentiated between forest core and forest edge, defining forest edge as a 20 m wide band where forest polygons bordered non-forest land cover. We conferred with experts familiar with local pollinating insect taxa and used an iterative process to arrive at consensus values for land cover that express categories' relative habitat suitability for the representative pollinating bee species occurring in Oslo. Land cover categories that are incapable of providing either floral resources or nesting sites (e.g. water surfaces or densely built areas) were valued at or near zero. Land cover categories that represent the best possible habitat within the study area were valued at 1. Based on the experts' contention that nesting site availability was far less likely to limit populations of pollinating insects in Oslo than floral availability, we chose to simplify the ESTIMAP model for Oslo by using a combined habitat suitability score. Habitat suitability values also attempted to capture variation in the temporal availability of floral resources, such that only land cover categories expected to offer the most continuous availability of floral resources received full habitat suitability value (1).

We first used the ESTIMAP pollination spatial model for Oslo to calculate a habitat suitability score for 25 m raster cells. However, our preliminary validation analyses from insect sampling (described below) indicated that the spatial data provided by the municipality failed to capture the large degree of heterogeneity we observed in vegetation cover within many of the land cover categories. We therefore applied imagery from the Sentinel 2 satellite (at 10 m resolution) to improve the detail of the information in the land cover classes from the municipal land cover data. Sentinel 2 data included 13 spectral bands, plus Normalised Difference Vegetation Index (NDVI). We used a Random Forest classifier in R Studio (Rstudio Team, 2016), based on 10 000 training points, to classify the imagery into five land cover classes. These classes included 1) Agriculture (low uniform vegetation that may include mowed grass); 2) low (non-tree) vegetation; 3) tree canopy; 4) built-up infrastructure (buildings, roads and other artificial surfaces) and 5) water. The method achieved an 86% classification accuracy. We then designated value adjustments for each combination of municipal and Sentinel 2 land cover categories (Table 1), consulting with experts to verify these value adjustments, and recalculated the ESTIMAP pollination model at a 10 m resolution. We chose to retain the heterogeneity that Sentinel 2 satellite data provided by removing the flight distance component from the original ESTIMAP model.

Roadside vegetation often includes high densities of flowering plants, including many species that are popular amongst pollinators. Yet vehicle exhaust can disrupt bees' ability to detect floral odours (Girling et al. 2013), pollination rates can decrease as traffic speeds increase (Dargas et al. 2016) and collisions with vehicles may lead to increased bee mortality (Kallioniemi et al. 2017). We therefore attempted to capture the detrimental effects that greater levels of automotive traffic could have on pollinator foraging by generating a value-reduction layer based on cells' proximity to aboveground, high-traffic roads (defined as Motorways, Freeways and Major roads in the Teleatlas® Multinet™ Dataset, 2013). We used an exponential decay function, with habitat suitability values reduced by 0.2

immediately adjacent to high traffic roads with the effect diminishing to zero at 200 m distances from road edges.

Table 1.

Habitat suitability scores for land cover categories

Land cover category (from municipal data)	Pixel habitat suitability score based on Sentinel 2 satellite land cover classification				
	Agricultural	Low vegetation	Tree	Built	Water
core FNF (forest with no floral resources)	0.1	0.4	0.1	0.1	0.05
core CO (conifer forest)	0.2	0.6	0.3	0.1	0.05
core OF (other forest)	0.3	0.5	0.4	0.1	0.05
core MFL (mixed forest low)	0.4	0.6	0.5	0.1	0.05
core MFH (mixed forest high)	0.3	0.8	0.6	0.1	0.05
core BLF (broad leaf forest)	0.3	0.7	0.6	0.1	0.05
core FYF (forest with floral resources)	0.4	0.7	0.7	0.1	0.05
edge FNF (forest with no floral resources)	0.5	0.4	0.3	0.1	0.05
edge CO (conifer forest)	0.6	0.9	0.8	0.2	0.05
edge OF (other forest)	0.5	0.7	0.6	0.2	0.05
edge MFL (mixed forest low)	0.6	1	0.9	0.2	0.05
edge MFH (mixed forest high)	0.6	1	0.9	0.2	0.05
edge BLF (broad leaf forest)	0.7	1	1	0.2	0.05
edge FYF (forest with floral resources)	0.7	1	1	0.2	0.05
agricultural land	0.3	0.6	0.6	0.1	0.05
medium built areas	0.7	0.7	0.6	0.1	0.05
densely built areas	0.35	0.45	0.25	0.05	0.05
mines	0.35	0.55	0.35	0.05	0.05
graveyard	0.5	0.9	0.7	0.1	0.05
industrial	0.4	0.6	0.4	0.05	0.05
Transportation-infrastructures	0.5	0.8	0.5	0.1	0.05
Sports-stadiums	0.1	0.1	0.4	0.1	0.05

alpine ski area	0.4	0.5	0	0.1	0.05
parks	0.5	0.6	0.8	0.1	0.05
golf course	0.4	0.5	0.7	0.1	0.05
pastures	0.2	0.3	0.6	0.2	0.05
semi-natural vegetation	0.7	1	0.8	0.2	0.05
open areas	0.7	1	0.8	0.2	0.05
bogs	0.4	0.4	0.3	0.1	0.05
freshwater	0.4	0.2	0.4	0.1	0.05
ocean	0.3	0.3	0.3	0.05	0.05

2.3 Assessing honeybee foraging pressure

To model the distribution of domestic honeybees foraging in Oslo, we used the exact locations of permanent beehives provided to us by the ByBi beekeepers’ organisation and the number of hives per location. Honeybees—like all bee species—are central location foragers and travel only as far as necessary to collect food from flowers to minimise energy expenditure and mortality risk (von Frisch 1967, Seeley 1995). Honeybee spatial foraging patterns have often been modelled as approximate diffusion functions based on an average flight distance, even though it is widely acknowledged that honeybee foraging varies according to the spatial distribution of flowering resources and the flowering phenology of local plant species (Couvillon et al. 2014). For the scope of the present study, however, we sought a coarse estimation of potential honeybee foraging pressure over an entire growing season, using a simple diffusion model that assumes a homogeneous distribution of floral resources throughout the landscape. Couvillon et al. (2014) and Garbuzov et al. (2015b) used waggle dance analyses (von Frisch 1967) to generate probability maps of bee foraging patterns in Brighton, UK: an urban landscape with a population density similar to that of Oslo (3 445 ind · km²). They then used the distribution of points on these maps to model the probability of a site's visitation as a function of the site's distance from the hive. We used the parameters from the model presented by Couvillon et al. (2014) to generate a raster layer (10 m pixels) for the potential relative distribution of foraging honeybees using an exponential decay function:

Honeybee foraging abundance = $N * e^{(-0.002 * D)}$,

where N = number of beehives at a given location and D = distance (m) from a given beehive location. We then divided the results of this expression by the maximum value so that all pixels scores ranged from 0 to 1. We subsequently identified regions within the municipality where foraging honeybees could have a comparatively greater potential to exhaust floral resources by subtracting ESTIMAP habitat suitability scores from foraging honeybee abundance scores. Pixels with values close to 1 indicate high honeybee to floral resource ratios, implying a greater potential for competition with wild bee species.



Figure 1.

Pan trap used to collect flower visiting insects.

We used GRASS GIS 7.2.0 (Grass Development Team, 2016) and QGIS 2.18.6 (QGIS Development Team 2017) for all GIS data preparation and analysis.

2.4 Field work for model validation

We collected pollinator specimens using pan traps, a common passive method used for sampling bees (Kearns et al. 1998, Dafni et al. 2005), using a trap design adapted from the bee monitoring protocol described in LeBuhn et al. (LeBuhn 2002) and Westphal et al. (Westphal et al. 2008). Traps consisted of three 500 ml plastic soup bowls painted with blue, yellow and white UV-bright paint (colors #3107, #3104 and #3108; Sparvar Spray-Colour GmbH, Merzenich, Germany), and containing approximately 250 ml diluted detergent solution. We mounted one bowl of each colour on wooden stakes and placed them approximately level with flowers in the surrounding vegetation (Fig. 1). We selected trap locations with the intention of capturing the range of habitat suitability values as expressed in an early version of our ESTIMAP model, at 74 sites distributed throughout Oslo's built zone. We deployed one trap at each site on dates in either June (24 sites), July (20 sites) or August (30 sites) in 2015, sampling on warm days ($> 15^{\circ}\text{C}$) with abundant sun, no precipitation and low winds. Collection periods lasted two complete daylight cycles and we retrieved traps 48 hours after they were first deployed. We therefore refer to a single trapping event as a "trap date." After each collection period, we strained the contents of all pan traps and placed them in watertight bags and froze the specimens until further processing. We sorted specimens by morphotype and recorded the abundance of each morphotype, later identifying specimens from the Apoidea superfamily to species. We then used linear regression to assess whether actual pollinator community biodiversity reflected habitat suitability scores from the ESTIMAP-pollinator map for Oslo. We compared bee community abundance and species diversity with the high resolution (10 m pixel) ESTIMAP model's mean score for all pixels within a 50 m radius of trap locations. We also used linear regression to explore whether the number of honeybees captured in traps reflected our simplistic model for honeybee foraging abundance, calculated as the mean relative

abundance for all pixels within both a 50 and 500 m radius of trap locations. Finally, we used linear regressions comparing honeybee and wild bee abundance and species richness to assess the correspondence between honeybees and wild bee distributions. We used SPSS (version 23.0) for all statistical analyses, and verified that the data met all necessary assumptions for each test.

Results

The 74 trap dates yielded 2730 insects >4 mm long, with most insect captures (1933 individuals) belonging to the order Diptera (flies). Traps captured 395 individual bees—including 83 honeybees, 81 solitary bees and 231 bumblebees. Honeybee and solitary bee captures were highest for the July collection period (2.1 and 1.8 bees trap⁻¹, respectively) while bumblebee captures were greatest in August (4.7 bees * trap⁻¹). Total bee abundance ($F_{1,72} = 4.93$, $P = 0.03$), bee species richness ($F_{1,72} = 5.16$, $P = 0.03$), and bumblebee abundance ($F_{1,72} = 4.88$, $P = 0.03$) all increased with increasing ESTIMAP habitat suitability scores for areas within a 50 m radius of trap locations (Supplementary material). Solitary bees' abundance ($F_{1,72} = 0.39$, $P = 0.54$) and species richness ($F_{1,72} = 0.03$, $P = 0.95$), and honeybee abundance ($F_{1,72} = 2.83$, $P = 0.10$) did not vary significantly with habitat suitability as expressed in the ESTIMAP model. The abundances of honeybees collected in traps did not vary significantly with the values from the foraging abundance model for the areas within either 50 ($F_{1,72} = 0.29$, $P = 0.59$) or 500 m ($F_{1,72} = 0.28$, $P = 0.58$) radii from trap locations. We found no evidence that greater numbers of honeybees were negatively associated with the abundance or species diversity of wild bees. Total bumblebee abundance ($F_{1,73} = 9.64$, $P = 0.003$), bumble species richness ($F_{1,73} = 7.26$, $P = 0.01$), solitary bee abundance ($F_{1,73} = 8.34$, $P = 0.005$) and solitary bee richness ($F_{1,73} = 4.20$, $P = 0.04$) corresponded positively with honeybee abundances.

Our map of pollinator habitat suitability illustrates a considerable spatial heterogeneity within Oslo municipality (Fig. 2). The heavily developed city centre presumably provides relatively few floral resources for insect pollinators. However, the model does indicate higher habitat suitability provided by the park-like gardens surrounding the Royal Palace as well as a number of other, smaller parks within a 1.5 km radius of the city's centre. The map also illustrates a swath of low habitat suitability values extending from the city centre to the northeast, corresponding with areas of dense commercial and industrial infrastructure and high levels of automobile traffic. As our model includes satellite-derived high-resolution spatial data, however, we can also detect the presence of numerous collections of pixels with high habitat suitability scores along this corridor (Fig. 2, inset). Exclusion of the flight component of the original ESTIMAP model structure also substantially raised the coefficient of variation for pixels' habitat suitability scores (53.1 with the flight component versus 79.56 without).

Our model for foraging honeybee abundance (Fig. 3) identifies the greatest density of honeybees at both the southwest and northeast of Oslo's city centre. Fig. 4 illustrates areas within the study area where the abundance of foraging honeybees may have a greater

potential to exceed local floral availability. Foraging honeybee pressure is greatest in the city centre, where both habitat suitability scores tend to be lower and beehive density is highest. The model indicates relatively low expected pressure from foraging honeybees in three of the six precautionary areas proposed by the Oslo Urban Environmental Agency located within the municipality's built zone. The model also predicts relatively low honeybee expected foraging pressure in the lower half of the largest sensitive area that extends along the eastern shoreline of the Oslo fjord.

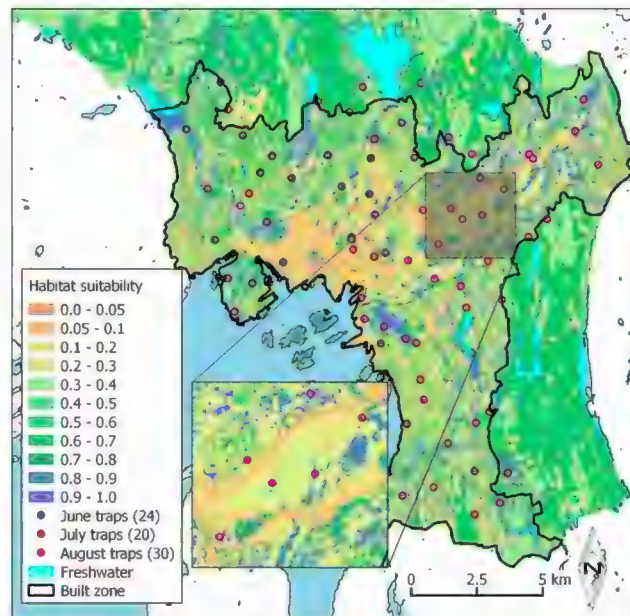


Figure 2.

Map of pollinator habitat quality scores and locations of pan traps used for model validation.

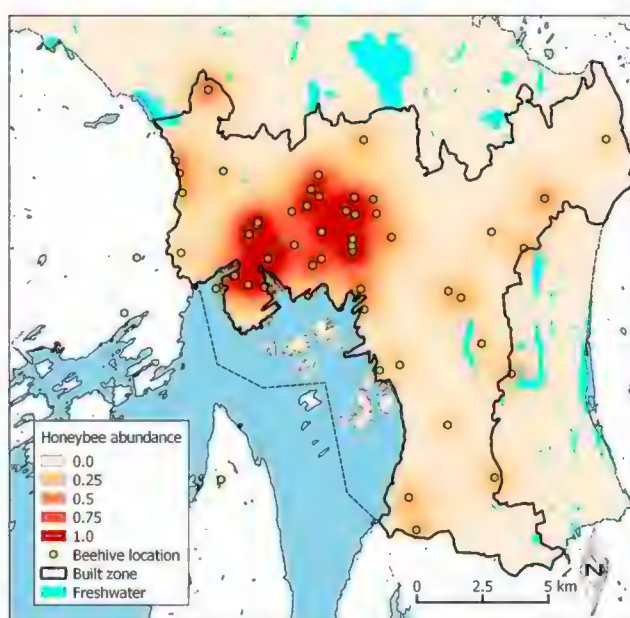


Figure 3.

Map of relative honeybee foraging densities and locations of beehives.

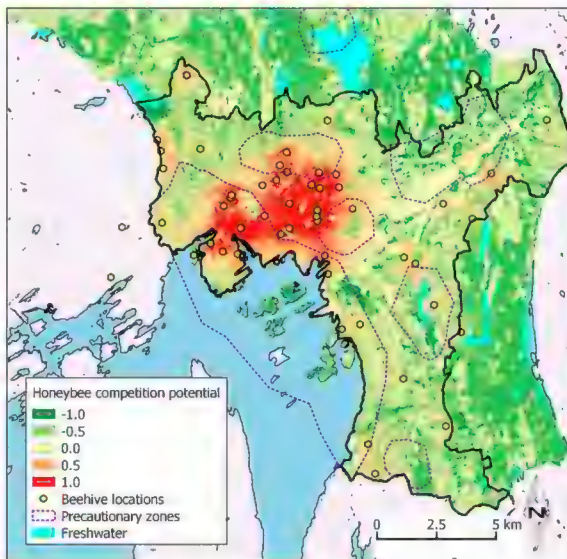


Figure 4.

Map of the relative resource demand of foraging honeybees, accounting for the floral resource availability of the Oslo municipality landscape. Precautionary zones represent areas proposed by Oslo Urban Environmental Agency to protect potentially sensitive populations of red-listed wild bee species from competition with domestic honeybees.

Discussion

4.1 Modelling pollinator habitat suitability

The version of the model we present in Fig. 2 represents a highly adapted version of the ESTIMAP model for predicting the pollination potential at the European continental scale (Zulian et al. 2013). We sought to develop an appropriately parsimonious model to describe local variation of resources that determine urban and peri-urban pollinator abundance. We eliminated the model component pertaining to climatic effects on bee activity rates, reasoning that the variation in microclimates within Oslo's are most likely insufficient to justify including it in the model. The scientific literature contains strong evidence that food resource availability is the predominant factor regulating bee populations, and little clear evidence that other factors—such as nest site availability—are commonly limiting (reviewed by Roulston and Goodell (2011)). We therefore opted to not parse land cover suitability scores into both floral resources and nesting site components, but rather use a single score based primarily on floral resource availability. We recognise that this is a modification which may not be appropriate for all urban areas. Cavity-nesting bee species in urban areas can experience nest-site limitation (e.g. Potts et al. 2005, Steffan-Dewenter and Schiele 2008), although cavity-nesting species can also be more abundant in urban areas than in suburban sites or natural habitats (Matteson and Langellotto 2009, Cane et al. 2006, Zanette et al. 2005). Ground-nesting species that constitute the majority of wild bee species (Winfree 2010) may also experience nest site limitation in urban areas, particularly for areas with low proportions (<10%) of permeable surfaces (Fetridge et al. 2008, Matteson and Langellotto 2009). However, the pollination experts we consulted contended

that Oslo's high proportion of areas with permeable surfaces and considerable tree cover provides sufficient nesting substrate for both ground- and cavity-nesting species, effectively making nest site limitation non-existent in our study area. We therefore contend that using a score that reflects experts' assessment of the overall suitability of land cover area will more appropriately reflect variation in the factor that is most likely to have the greatest impact on the urban bee community as a whole.

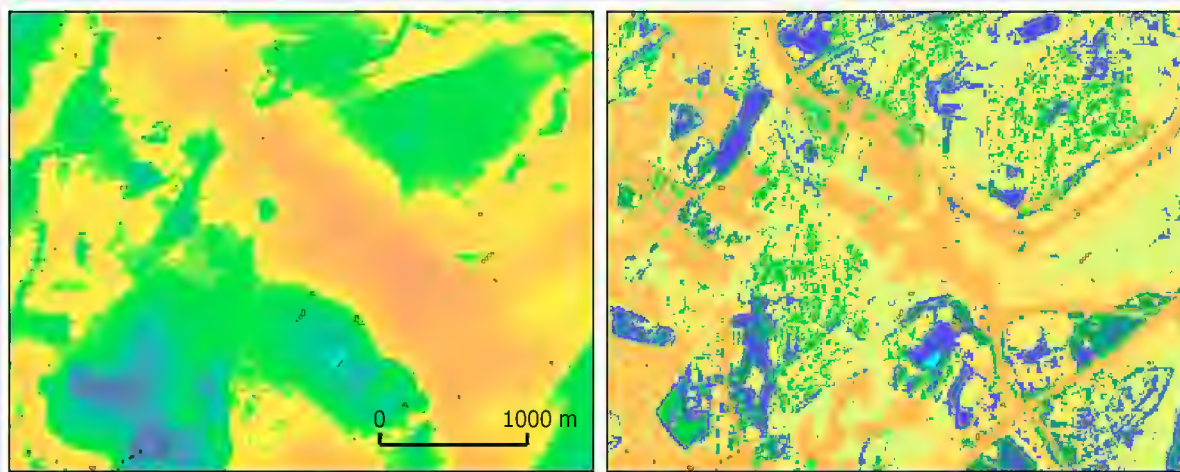


Figure 5.

Frames of the same portion of Oslo municipality, contrasting the detail provided in an earlier version of the ESTIMAP model that included a component simulating bees' foraging distance (left) and the final version with the foraging distance component removed (right).

We also modified the original ESTIMAP model by eliminating the flight distance component, which is a change that we contend may be an appropriate approach for other models of pollinating insect abundances. We recognise the intuitive appeal with accounting for foraging flight in pollinator distribution models: bees are central place foragers and must bring food back to their nests to feed their offspring (Westrich 1996). Bee species also have different foraging ranges (e.g. Walther-Hellwig and Frankl 2000, Gathmann and Tschardt 2002), with maximum foraging distances that generally vary according to body size (Greenleaf et al. 2007). The InVEST (or Lonsdorf) pollination model, on which the continental-scale ESTIMAP model was based, predicts the relative abundances of bees in landscapes by starting with the spatial arrangement of nesting sites and then estimating floral patch visitation rates based on the distance between patches and nesting habitat (Lonsdorf et al. 2009). Both models treat pollinator flight as a simple diffusion function originating from nest sites. In the case of the continental-scale ESTIMAP model, the mean foraging distances for different bee species groups (500 to 1 500 m) was equal or only slightly greater than the spatial resolution of the land cover data. Landscape cover at this resolution is also more homogeneous at this scale, so incorporating flight distances at these spatial scales has very little effect on the model output (Olsson et al. 2015). When the spatial resolution of land cover data is higher, however, treating foraging movements as a simple diffusion model has a smoothing effect on pixels' habitat quality values as evidenced in the difference in coefficients of variation between models with and without the flight component (Fig. 5). This can be particularly unfortunate in complex landscapes like Oslo and many other urban settings. The smoothing effect we observed in the ESTIMAP

model for Oslo before we removed the flight distance component effectively masks much of land cover's spatial heterogeneity and thereby hides the presence of small patches with high habitat suitability (Fig. 5).

The Lonsdorf model performs reasonably well at the landscape scale in coarse grained or homogeneous landscapes (Lonsdorf et al. 2009), however it performs less well in more heterogeneous (complex) landscapes (Davis et al. 2017, Grafius et al. 2016, Kennedy et al. 2013). Olsson et al. (2015) argue that this is because the Lonsdorf model does not include a behavioural mechanism to simulate how bees forage selectively in areas with higher resources. Empirical studies of bee foraging patterns demonstrate that bee densities depend on both local habitat quality and the quality of the surrounding habitat (Steffan-Dewenter et al. 2002, Carvell et al. 2011, Woodcock et al. 2014). Yet the effects surrounding habitat can have on the importance of a given patch are complex. Large continuous areas of high quality habitat provide foraging bees with a greater total resource base (Goulson et al. 2010), but the ample abundance of resources can also diminish the relative importance of any single portion of the larger area (Holzschuh et al. 2011). Whereas isolated patches of high quality habitat surrounded by area of lower quality could serve to concentrate the abundances of pollinators (Kallioniemi et al. 2017, Kovács-Hostyánszki et al. 2013). Olsson et al. (2015) therefore propose adding a central place foraging (CPF) behavioural mechanism component to the Lonsdorf model framework to better account for bees' selective use of high value habitats in complex landscapes. When tested on both synthetic and real landscapes, the Lonsdorf and CPF models predictions diverged with the increasing complexity of the landscapes used for simulations. In complex landscapes, the CPF model described far more within-patch variation in visitation (Olsson et al. 2015).

The insect sampling which we conducted to validate our ESTIMAP model of bee habitat suitability confirms why models should not obscure the fine-grained spatial detail of floral resource distribution. Our traps' captures generally reflected the habitat qualities of their immediate surroundings (within ≈ 50 metres) and corresponded less to trap sites' larger landscape context. In other words, our trapping revealed high abundance and richness in small patches with ample flowers, even when these patches lay within larger areas dominated by low-suitability habitat. The Lonsdorf (Lonsdorf et al. 2009) and ESTIMAP-continental scale models manage to describe general quality of the landscape and even identify broader hotspots of exceptionally high quality habitat. However, they would presumably both miss the landscape's finer nuances that are evident in the Oslo model when the flight component is removed (Fig. 5). By accounting for the metabolic costs, mortality risks and foraging rewards that ultimately determine bee foraging behaviour, the CPF model presumably captures the spatial heterogeneity of floral resource utilisation and thus the spatial variation in bee densities. However, it also represents a considerable increase in model complexity and it may over-emphasise the relative importance of nesting site availability or the spatial separation between nesting sites and floral resources in many environments. Given the general lack of evidence that nesting site availability commonly limits bee populations (Roulston and Goodell 2011, Torné-Noguera et al. 2014), we question whether many pollinator modelling applications are well served by adding this

complexity. Our contention is that a model of flower resource availability, using the highest resolution data available, provides a more parsimonious representation of the factor most likely to determine variation in densities amongst the broader pollinator community. A floral resource-based model also has the incidental advantage of being easier to communicate to non-scientists.

Investigations of urban bee communities underscore the important role that small, resource-rich patches play in supporting urban area's wild bee populations (Saure 1996, Tommasi et al. 2004, Frankie et al. 2005, FetrIDGE et al. 2008, Matteson and Langellotto 2009). While studies often report decreased pollinator populations from urbanisation (Ahrné et al. 2009, Bates et al. 2011, Matteson et al. 2013), numerous studies also show a positive effect of urbanisation on certain bee taxa (Tommasi et al. 2004, Winfree et al. 2007, Carré et al. 2009). For bumblebees in particular, urban areas can harbour greater species richness than rural or natural areas (Gunnarsson and Federsel 2014, Baldock et al. 2015). These patterns are often attributed to the high degree of heterogeneity found in many urban areas (Banaszak-Cibicka and Żmihorski 2012). For cities like Oslo, which has a comparatively high proportion of permeable surfaces, urban development can also produce intermediate levels of habitat fragmentation and result in greater amounts of highly suitable edge habitat than can be found in rural landscapes (Winfree et al. 2007, Carper et al. 2014).

4.2 Honeybee competition potential

Our empirical measures of bee abundance in Oslo provided no clear evidence of instances at trap sites where high numbers of honeybees appeared to displace wild bee species. In general, sites with greater numbers of honeybee also contained higher wild bee abundance and richness. Gunnarsson et al. (Gunnarsson and Federsel 2014) also found positive co-variations of honeybees and bumblebees in urban gardens and flower beds located in Gothenburg, Sweden. They concluded that resources at the study sites were sufficient to avoid significant competition between the two groups. Yet we cannot exclude the possibility that our sampling failed to capture instances where honeybee abundances were locally far higher and capable of effectively excluding wild bees. Honeybees have the capacity to communicate the location of particularly profitable forage to mates (Seeley 1994). When foraging individuals discover a high resource area, a colony can mobilise large numbers of its foragers to seek and exploit that site together. It appears that our sampling methods did not capture any such events, and we are unable to assess how likely or frequent they might occur within the Oslo municipality.

Our work identified areas in Oslo where the impact of honeybee abundances is greatest relative to the distribution of floral resource availability (Fig. 4). We wish to stress, however, that we have no evidence that honeybees are exhausting the floral resources at these areas. Habitat suitability scores reflect relative values of general floral availability and are not estimates of actual floral ability per unit area. Actual floral availability data would enable the creation of bioenergetics models for Oslo's insect pollinator community, like those presented by Dicks et al. (Dicks et al. 2015) and Carvell et al. (Carvell et al. 2011) and

enable the calculation of how honeybee colonies' nutritional demands for pollen and nectar compare with the volume of available resources.

Several recent studies employing manipulative experiments report evidence of competition between honeybees and wild bees, yet the details of the work suggest that the same dynamics may not be occurring in Oslo. Lindström et al. (Lindström et al. 2016) found that adding honeybee colonies to fields in nearby Sweden depressed the densities of wild insects in a field of oilseed rape (*Brassica napus* L.), despite massive floral resource availability within the crop. The agricultural landscapes of southern Sweden, where the study took place, are far more homogeneous than the Oslo municipality and are largely devoid of natural or semi-natural vegetation. The magnitude of the manipulation was also intended to simulate the dynamics of using honeybees in commercial scale agriculture (12 - 43 beehives within fields between 10 and 20 ha). The authors do not provide the fields' actual densities (hive · ha⁻¹), but the number of hives suggest that treatments resulted in honeybee colony densities that exceed those found anywhere within Oslo municipality. The largest number of beehives at any location for 2016 in Oslo was nine, with most locations having three hives or fewer. In another recent Swedish study, Herbertsson et al. (Herbertsson et al. 2016) found that honeybee addition suppressed bumblebee densities in the vegetation surrounding agricultural fields, however the effect was dependent upon the amount of natural vegetation present. Honeybee additions suppressed bumblebee densities in field borders and road verges adjacent to field in homogeneous landscapes, but not in heterogeneous landscapes defined as having >4% semi-natural grasslands. None of the locations that form the basis for the precautionary zones has less than 4% semi-natural vegetation.

The honeybee addition treatments in Thomson (Thomson 2004) better simulate the densities of honeybees in Oslo municipality (1 – 2 hives per site). Honeybee additions decrease bumblebee foraging returns for both nectar and pollen, with negative effects on the male and female reproductive success that increased with proximity to honeybee hive locations. The study took place in dry coastal shrub vegetation at Big Sur (California, USA) and investigated a short-tongued bumblebee species (*Bombus occidentalis*) that forages on a list of plant species that had a 50% overlap with honeybees. Visitation overlap between honeybees and *B. occidentalis* reached >80% towards the end of the flowering season as soil moisture and nectar became scarce. Thomson (Thomson 2004) concludes that nectar, rather than pollen, was limiting for the bees in this system, as both bee species predominantly visited an abundant plant species (*Eriophyllum stachaeifolium*) that produces copious amounts of pollen but more limited amounts of low-quality nectar. Oslo receives ample precipitation throughout the summer, rather than a dry season like the study site used by Thomson (Thomson 2004), so it might seem unlikely that competition arising from such extreme moisture scarcity is likely to occur in there. However, we did observe honeybees stealing nectar in clover fields, so we cannot rule out nectar scarcity in Oslo as well.

The few examples of studies that explored competition between honeybees and solitary bees also failed to demonstrate clear evidence of negative effects of honeybees. Feral honeybees did not affect the reproductive success of a native Australian solitary bee (*Megachile spp.*), which the authors reasoned may be due to the native bee's tolerance for extremely high summer temperatures (Paini et al. 2005). Honeybees are native to Europe, so wild bee species are unlikely to have similar competitive advantages over honeybees in Oslo. And while stem nesting solitary bees foraging on heather (*Calluna vulgaris*) in northern Germany were less abundant on sites with honeybee hives, researchers were unable to detect any resulting negative effects on reproduction success for either stem nesting or ground nesting wild bee species (Hudewenz and Klein 2013). Reviews by Goulson (2003) and Paini (2004) fail to find consistent evidence that competition from honeybees has negative effects on native bee populations, although Cane and Tepedino (2016) suggest this may be due to the short durations and limited spatial scales of investigations. Cane and Tepedino (2016) estimate that a colony of honeybees from a wildland apiary is capable of collecting enough pollen to feed 110 000 progeny of an average-sized solitary bee (range 92 000 – 300 000). Wild bees alone are capable of removing virtually all the daily available pollen (Schlindwein et al. 2005, Larsson and Franzen 2007, Carvalho and Schlindwein 2011), indicating that pollen can be a limiting resource. While Cane and Tepedino (2016) recognise that the effect of wildland honeybees colonies on native bee populations will be largely contextual, their work provides compelling evidence that honeybees are potentially capable of negatively impacting wild bees, especially specialist species whose foraging choices overlap with honeybees.

4.3 Future research

The assessment we present here is admittedly incomplete as a means of determining the actual threat urban honeybees pose for the conservation of certain wild bee populations. We recommend two sampling approaches to further assess the vulnerability of wild bees in Oslo municipality. Figure 4 identifies the areas where competition from honeybees is most likely, and where future sampling efforts could be made more effective through concentrating on a smaller portion of the city's landscape. More focused insect trapping within these areas could reveal whether we actually see negative co-variation between honeybee and wild bee abundances that would indicate competition. We will conduct visual observations along transects at pan trap locations to verify data collected from pan traps and ensure that recorded observations include species that may not be susceptible to trapping. Visual observations will also allow us to assess the degree of resource overlap between honeybees and wild bees as demonstrated by which flowers different bee species are visiting. At the conservation priority sites that comprise the basis for precautionary zones, visual (non-destructive) assessment of bee abundance and resource use should also be conducted to estimate the intensity of honeybee foraging pressure at these sites.

The ESTIMAP model for Oslo can structure field surveys of urban vegetation according to the scores for habitat suitability (or floral availability). Information on the species identities of flowering plants, as well as the temporal availability (or phenology) of flowering resources, would serve as both a model validation and enhance the model's capacity to

describe distribution of biodiversity values within Oslo municipality. The Oslo Urban Environmental Agency has expressed an interest in this kind of information to help with urban planning, since it does not presently exist. Ideally, future vegetation surveys would include measurements of flower abundances and their variation through the growing season. Data on flowering plant communities' species compositions, productivity and phenology would enable us to generate estimates of the landscape types' supply of nectar and pollen. We could then compare floral resource supply with honeybees' nutritional needs (per colony) and thereby assess the ecological footprint of urban beekeeping in Oslo. Modelling the appropriate honeybee stocking density for zoning purposes deserves further attention.

Another central research question that remains is how far do honeybees tend to fly from their hive locations, based on the distribution of floral resources in Oslo municipality. This information would determine the likelihood that honeybees will visit sites with conservation priority in abundances that would lead to competition with threatened wild bee species. Although we parameterised our model for honeybee abundance with empirical measurements of honeybee foraging, we readily acknowledge that our use of a simplistic diffusion-function may not be appropriate for the distribution of floral resources in Oslo and is worthy of the same criticisms we directed at the Lonsdorf and ESTIMAP continental-scale models. Using a CPF model based on our data on actual beehive locations, beehive numbers and the spatial patterns of suitable foraging habitat would most likely generate honeybee abundance predictions with greater spatial heterogeneity. However, both the Lonsdorf and the CPT models are highly sensitive to a parameter expressing the average distance a bee would travel. As we discussed earlier, bees' average flight distance is not only a function of an individual's physical capacity but also the actual need to seek food resources at greater distances from nest sites.

Fortunately, honeybees' means of communicating foraging resource locations to other colony members via "waggle dances" provides us with a tool for estimating flight distances within a given landscape (von Frisch 1967, Couvillon et al. 2012). The bees' dances encode a vector from the hive to the location of food resources, which researchers can recode using slow-motion films of dancing bees. By compiling analyses of dances over an entire growing season, it is possible to obtain integrated information about where a colony or group of colonies is foraging and how foraging might change with time (Visscher and Seeley 1982, Beekman and Ratnieks 2000, Garbuzov et al. 2015b, Balfour and Ratnieks 2017). By analysing the agreement between the ESTIMAP model of habitat suitability and waggle dance-derived foraging probability maps at one or more sites, we could determine whether the ESTIMAP model can sufficiently predict where honeybees are likely to forage based on a given hive placement and the number of colonies located there. This information would also be highly valuable for beekeepers who could select site locations based on proximity to high quality foraging sites. Decoding waggle dances from colonies located within hypothetically attainable distances from sites with conservation priority (anything from 1 to 5 km distances), would reveal what the appropriate buffer distance to use for precautionary zones. Decoded waggle dances from beehives located in the proximity of the Oslo fjord (<1km) could reveal whether or not the open water between

islands deters honeybees seeking floral resources on the islands in the fjord. Many of these islands have high conservation significance, and the 1 km buffer around them is why the largest precautionary zone is the size it is.

Research involving waggle dance decoding often involves assessing the type and amount of pollen found on the the legs of dancing bees, since this provides information about which flowers bees are utilising at a given site and whether the dancing bee is advertising sources or nectar or pollen (Couvillon et al. 2015). Researchers can also collect pollen from beehives and identify it morphologically (Coffey and Breen 1997), or by techniques made possible with new advances in DNA barcoding (Galimberti et al. 2014, Bell et al. 2016) to determine which plant species honeybees utilise and how the composition of pollen bees collect varies during the flowering season. DNA barcoding of collected pollen may also be able to reveal the extent to which honeybees utilise pollen from the rare plant species that are food sources for rare specialist wild bee species.

4.4 Additional implications for management of urban biodiversity

One of the underlying goals of this study was to test the ability of the ESTIMAP model to express variation in the landscape that presumably determines variation in urban pollinator abundance and richness. Our empirical measurements from trap collections of the wild bee community partially predict the ESTIMAP habitat suitability output. Due to bees' integral role in the reproduction of flowering plants, bees can function as indicator species for the status of the flowering plant community (Kevan 1999, Couvillon and Ratnieks 2015). The distribution of habitat suitability scores (Fig. 2) can therefore serve as a useful presentation of the spatial variation in Oslo's broader urban biodiversity. Urban planners may use maps of pollinator abundances to identify greenspace areas with particularly high biodiversity values that are worthy of protection from future development, as well as areas where biodiversity values may be lacking and would benefit from restorative measures.

Bees' ability to capitalise on small patches within the urban environment offer opportunities for small habitat improvement measures to yield large benefits (Hall et al. 2017). Compared with larger mammals that are often targets of conservation efforts, the functional ecology of pollinating insects corresponds with substantially more modest habitat requirements. Urban residents can both understand and personally contribute to the simple measures needed to increase areas' habitat suitability for pollinating insects. Actions like sowing seeds or merely altering mowing regimes can convert flower-poor grasslands on public and private lands to areas providing greater amounts of flowers that are attractive to pollinators (Blackmore and Goulson 2014, Garbuzov et al. 2015a, Smith et al. 2015, Beumer and Martens 2016). Shifting to meadow management on grass-covered slopes in public parks in Oslo would also provide larger foraging areas while avoiding conflicts with sports recreational uses. Seemingly low-value or marginal areas like road verges, power lines and railway banks also have the potential to provide valuable infrastructure for supporting pollinator populations (Berg et al. 2013, Potts et al. 2016). Such management approaches can both improve citizen engagement and contribute to a more sustainable urbanisation (Hall et al. 2017).

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